Doridoeides gardineri: a Doridiform Cladohepatic Nudibranch.

By

Sir Charles Eliot,
Vice-Chancellor of the University of Sheffield;

and

T. J. Evans,
Lecturer in Zoology in the same University.

With Plates 15 and 16, and one Text-figure.

The nudibranchiate mollusc which forms the subject of this paper presents an unusual combination of characters. It has the external appearance of a Dorid, except that it has no gills, but its digestive organs are arranged on the cladohepatic plan. It was originally described by Sir Charles Eliot as Doridomorpha gardineri in Mr. J. Stanley Gardiner's 'Fauna and Geography of the Maldives and Laccadives, Nudibranchiata,' pp. 544-5. Professor Bergh, however, has pointed out ("Ueber clado- und holohepatische nudibranchiate Gastropoden," 'Zool. Jahrb.' Bd. xxiii, Heft 6, p. 740) that Doridomorpha was used in 1832 by Audouin and Milne Edwards. The animal to which they gave the name cannot now be identified, but it is unfortunately incorrect according to the laws of nomenclature to apply it to a new form and Doridoeides is now proposed as a substitute of equivalent meaning.

The original description was made from a single specimen obtained by Mr. Stanley Gardiner in the Fiji Islands

(Rotuma). It was small (6·5 mm. by 5·5) and much hardened so that a satisfactory anatomical investigation was impossible. Mr. Crossland and Sir C. Eliot both examined it and could find no trace of a blood gland or of a second spermatotheca but, as those organs are characteristic of the Doridida, and as Professor Bergh had described them as present in Doridoxa, an externally similar gill-less doridiform animal. they did not venture to regard their absence as certain, and tentatively referred Doridomorpha to the Doridoxidæ, adding that it might possibly prove to be the type of a new family. An examination of more numerous and better preserved specimens obtained by Mr. Stanley Gardiner on his last journey to the Seychelles shows that this is the case. The second spermatotheca and blood gland are really absent and the animal has a ramified liver. It is, therefore, despite its general resemblance to Doridoxa, not very nearly allied to it and cannot be placed in the same family.

Doridoeides gardineri, sp. nov.

= Doridomorpha gardineri Eliot (in Nudibranchiata of J. Stanley Gardiner's 'Fauna and Geography of the Maldives and Laccadives,' vol. ii., part i, 1904).

Eleven specimens labelled Coetivy and preserved in formol. Coetivy is the southernmost island of the Seychelles group, and Mr. Gardiner's notes state that the nudibranchs obtained there were "all from the reefs, which differ from those of the Chagos archipelago in being almost completely covered with Zostera." It is probable that the animal adheres to the leaves of the Zostera and harmonizes with them in colour.

The natural shape seems to be flat and nearly circular, but the preserved specimens are bent in various ways and have the edges turned inwards. One which seems to have kept its form fairly well is 10 mm. long, 9 broad and 2 high. These are the average dimensions of the consignment. In the individual mentioned the foot is 6 mm. long and 3 broad, but

was evidently much wider in life as the margins are bent and rolled up. The free part of the mantle starting from its junction with the foot is 3·5 wide. It can be seen from the outside that about 2·5 mm. of this space are filled with dark internal organs and that only about 1 mm. of it corresponds to the mantle margin generally found in Dorids. The genital orifice is about 4 mm. from the anterior end, and the anus is about 2 mm. behind it.

The animals are of a greyish-green colour, a little darker in the centre where the internal organs show through, and lighter at the edges where there are none. Practically the coloration is uniform, though some specimens are lighter than others and the under side is usually rather lighter than the upper.

To the naked eye the dorsal surface appears to be smooth, but under a low power can be seen to be covered with small warts of various sizes, sometimes connected by an irregular reticulation and with minute pits between them. There is no median ridge and no trace of a branchial opening. The integuments are devoid of spines. The dorsal epidermis is thick and consists of several layers of cells: it is profusely pitted with mucus glands (fig. 2, *b*) and in many places rises into folds (fig. 2, *a*). On the under surface of the mantle and on the foot the epidermis is thin, but the foot is highly glandular. It contains both epidermal glands and subepidermal glands with granular contents and communicating with the exterior by long necks.

The rhinophores are completely retractile. Their pockets are simple holes without sheaths, visible to the naked eye; but in the sections it can be seen that the margins are slightly raised. As preserved, the pockets are often closed. When retracted the rhinophores often exhibit a few (6—7) strong transverse wrinkles or furrows, and these were also present in the specimen obtained at Rotuma. But they are probably not real perfoliations since they are absent when the rhinophores are completely exserted. In such cases the outline is even and cylindrical. There are no oral tentacles and nothing

which can be called a head. In some specimens the mouth is a simple orifice above the foot, but in others there is a sort of snout. It would seem, however, that this protrusion is due to artificial causes and is not a natural and permanent structure. There are no lamellæ on the under side of the mantle as in Phyllidia, etc., but it is uneven and in some cases presents ridges and bulges probably caused by the hepatic follicles. The foot is large, with ample expanded margins. The anterior margin is straight and not grooved.

When the internal cavity is opened, the central nervous system (fig. 3) is seen lying on the top of the œsophagus and surrounding it. There is no trace of a blood-gland. The cerebro-pleural ganglia (fig. 3, *a*) are rather large and elliptical. Externally they show no division but a section indicates that the ganglionic mass is of dual origin and divided internally by a constriction into two nearly equal ellipsoids. The pedal ganglia (fig. 3, *b*) are also elliptical and lie below and rather behind the cerebro-pleural. The buccal ganglia (fig. 3, *d*) are rather large, close to the pedal ganglia and also close to one another. No gastro-œsophageal ganglia could be found and no otocysts. The eyes are black and lie near the base of the rhinophores on the olfactory ganglia (fig. 3, *c*), the optic and olfactory nerves being apparently fused. This arrangement is unusual, but something similar may be seen in Bergh's figure (Malac. Unters. in Semper's 'Reisen,' Heft. xv, pl. lxxi, fig. 17) of the nervous system of Tritonia (Candiella) plebeia where the optic and olfactory nerves are joined for a considerable distance and separate only in their upper portion. The pigment layer of the eye lines a cup formed of a few large retinal cells, from which fibres run into the olfactory nerve at the base of its ganglion.

The jaws are yellowish but not deeply pigmented in any part, moderately convex, not very broad, united at the top by a hinge, and provided with short processes. The edge (fig. 4) is armed with a row[1] of very distinct projections with spatu-

[1] In the specimen described by Sir C. Eliot and Mr. Crossland two rows of broad denticles were found on the jaws, which were relatively wider, and the

late tips. Near the end of the row they appear thin and filamentous, possibly because they have become worn or folded on themselves. The radula (fig. 5, *a*) consists of about twenty-six rows, one or two of which are imperfectly developed and shadowy, with a constant formula of 4.1.4.[1] The teeth are neatly arranged in a close-fitting mosaic. The base of the large median tooth, which is arched and hollowed out behind, is nearly twice as broad as all the four laterals together. It bears a single cusp, large and only slightly bent downwards (fig. 5, *b*). The first lateral (fig. 5, *c*) is about three fifths the length of the median tooth but only a quarter of its breadth, with a single hamate cusp. The second and third laterals are similar but slightly smaller and more bent. The outermost tooth (fig. 5, *d*) is considerably smaller but more erect and stands up conspicuously at either end of the row. There are two salivary glands; their distal portions are expanded and spread over the genitalia and stomach. The left is much larger than the right. The remaining portion of each gland is band-like and terminates in a long thin duct which passes through the nerve collar and enters the posterior part of the buccal mass. Several glands, probably ptyaline, open into the buccal cavity, but they are embedded in the wall of the cavity and are not visible on its outer surface.

The œsophagus (fig. 6, *a*) is not long, and leads straight into the stomach, which is divided into two parts (fig. 6, *b* and *c*) by a constriction more marked on the right than on the left side. There is no structural difference in the walls of these two divisions, and neither contains any spines or plates, but as the hepatic ducts all open into the second division, the first should perhaps be regarded as a dilatation

radula, which was disarranged and in confusion, was estimated to contain 13 teeth in each row (i.e. 6 + 1 + 6). But these differences cannot be regarded as specific unless shown to be certain and constant. In Tritonia the number of rows of denticles in the jaw varies in several species, and the formula of the radula in the original specimen was doubtful. The shape of the teeth is the same.

[1] See footnote above.

of the œsophagus. Neither contained any solid food in any specimen. The intestine (fig. 6, *d*) issues from the mid-dorsal surface of the second division and, after describing a broad loop backwards and downwards, runs to the anal opening, which is an inconspicuous papilla on the right side, lying below the mantle edge and just at the point where it joins the body. The loop of the intestine bears a single longitudinal ridge resembling the typhlosite found in Lumbricus.

The stomach receives three hepatic ducts: one on the right (fig. 6, *e*), close to the exit of the intestine; one on the left (fig. 6, *g*), not quite opposite to it, but a little posterior; and one behind (fig. 6, *f*). The posterior and left ducts bifurcate close to the stomach and then ramify into branches composed of follicles which are not only found in the body cavity but enter the body wall and dorsal integuments, extending to within a short distance of the mantle brim. The arrangement and extent of the right duct is essentially the same, but the follicles are developed more luxuriously on this side than on the left, and the bifurcation is less clear, although the duct runs in two directions, backwards and forwards. The right and posterior branches anastomose, but though the right and left branches almost meet anteriorly they seem not to communicate, nor do the posterior and left branches. All three branches consist of variously shaped follicles communicating with one another, so as to offer a continuous passage but not forming a cylindrical tube except in the main ducts. For some distance from the point of entry into the stomach the walls of the main duct bear folds which dovetail into one another in the middle of the lumen and form a valve or strainer.

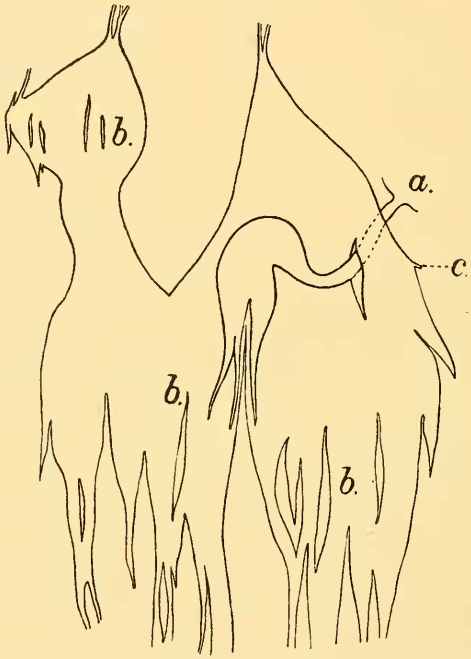
The cells which line the hepatic lobules are columnar or cubical and highly granular. Some are in a distended condition, others are attached to the wall of the lobule only by a strand or are free in its cavity. It would seem, therefore, that some of the liver cells are excretory in function, and are dropped into the follicle as they become extended with excreted material.

The heart (fig. 7) lies somewhat to the right of the median line. The walls are thin, and not strong. From the ventricle issue the anterior and posterior aortas, but the aortic system is not much developed, as is perhaps natural in an animal that has no gills. The arteries are thin, and do not extend beyond the level of the genital orifice in front and of the anus behind. The musculature of the ventricle also is feebly developed. The venous system is extensive and the veins are provided with valves (fig. 8) not only near the heart but in parts far from it, e. g. throughout the length of the lateral veins and venules and between the blood lacunæ of the foot. The auricle (fig. 7, *c*) has a large extension (fig. 7, *d*) on the left, enclosed by a corresponding extension of the pericardium; it adheres to the anterior part of the ventricle, the line of adhesion being zigzagged, and on the right it is attached to the wall of the pericardium.

The kidney (see text-figure) is a shallow chamber lying on the surface of the hermaphrodite gland, and sending downward prolongations between its follicles. In front it bifurcates like the hermaphrodite gland and is divided behind into a number of irregular tubes by the dorso-ventral muscles and the projecting genital lobes. The renal opening (*c*) is minute and near the anus. From the reno-pericardial opening (*a*) a tube passes dorsally through the substance of the kidney and dilates in the median line into a flattened vesicle. Posteriorly this sub-divides into three fine ducts, each opening into the kidney by a minute aperture. The wall of the kidney is formed by a layer of large, clear, cubical cells, the nucleated protoplasmic portion of which is limited to a small quantity at the base of the cell.

The genitalia (fig. 9) are large, and occupy most of the right-hand side. The hermaphrodite gland (fig. 9, *a*, and fig. 10) consists of a single undivided mass of roughly triangular shape, bifurcating in front so as to enclose the ampulla and the spermatotheca in the fork. It is traversed by branches of the liver, which enter it from below, by the dorso-ventral muscle bands (fig. 10, *d*) and by various pro-

longations of the blood lacunæ of the foot. The kidney (fig. 10, *e*) also sends prolongations into its upper surface. It presents a series of lobes the outer layers of which are formed by masses of ova (fig. 10, *b* and *c*). Within each lobe is an ample loculus (fig. 10 *a*), larger than the whole mass of ova, containing spermatozoa in all stages of develop-



Kidney of Doridoeides, seen from the dorsal side (× 22). *a*. Reno-pericardial opening. *b*. Gaps for passage of dorso-ventral muscles and protruding lobes of hermaphrodite gland. *c*. Renal opening.

ment. But there is no symmetrical arrangement of ovarian follicles round a central male follicle.

The hermaphrodite duct (fig. 9, *b*) is thin and short, but swells out into an unusually large pear-shaped ampulla (fig. 9, *c*), which again contracts into a thin tube. After a short straight course this tube (fig. 9, *f*) bifurcates. The male portion (fig. 9, *d*) runs forward and describes a com-

plete loop, after which it first dilates into a prostatic portion (but without any trace of a separate prostate gland) and then contracts into a muscular portion, terminating in a thin conical glans penis (fig. 9, *e*). No trace of spicules or other armature was found in this or any part of the genitalia. After the main bifurcation dividing the male and female branches, the female branch runs backwards for a little distance as a short tube and then itself bifurcates. A short duct leads to the spermatotheca (fig. 9, *g*), which is large, globular, and single, no trace of a second receptaculum seminis being found. The walls of the spermatotheca are thick, and produce a secretion. In some specimens small clumps of spermatozoa are embedded in this secretion. In others all the spermatozoa form a central mass in the main cavity of the spermatotheca. It is possible that the secretion serves to form small packets of spermatozoa or spermatophores. The spermatotheca communicates by a long thin duct with the vaginal opening (fig. 9, *h*) which lies at the base of the penis. The other division of the female branch enters the mucus [1] gland (fig. 9, *m*), enclosing the albumen [1] gland (fig. 9, *l*), which is smaller. The mucus gland communicates with the exterior directly by a slit-like irregular aperture (fig. 9, *i*) which lies a little behind the other orifices and is much larger than they are. Only spermatozoa are to be found in the ducts and in the spermatotheca. There are no ova except in the hermaphrodite gland, where they are in process of ripening or nearly ripe.

In all the specimens examined microscopically were found scattered cells which do not seem to form part of the essential bodily structure. They are large and rounded in outline, with vacuolated contents and a large round nucleus. They occur chiefly in the connective tissue spaces, in spaces hollowed out in the dermal muscle layers and among the epidermal cells. The fact that they are absent from the cavities of all the internal organs and from the lacunar blood spaces, and

[1] The functions of these glands are presumably as indicated by their names, but it is not easy to say which is which.

that they are limited to the dorsal regions of the body which are of a deeper green than the ventral surface, suggests that they are of the nature of Zoochlorellæ or symbiotic algæ.

We see no reason to doubt that this animal is specifically the same as that previously described under the name Doridomorpha gardineri. As noted above there are some discrepancies (which are, however, explicable) in the descriptions of the buccal parts, and the drawings of the teeth now published do not give quite the same impression as the simpler diagrams made by Mr. Crossland. But on comparing these teeth with those of the original specimen, which have been preserved, we can find no essential difference in shape.

The generic characters may be extracted from the above description and formulated as follows:

Doridoeides, gen. nov.

Form flat, doridiform. Dorsal surface smooth: no appendages of any kind except two rhinophores retractile into pits. No oral tentacles. Foot and mantle margin wide: anus lying between them on the right hand side. No blood gland. Heart somewhat to the right of the median line. Jaws distinct and denticulate. Radula narrow, consisting of a large strongly cusped central tooth and a few (4) laterals. Stomach without plates or spines. Liver system cladohepatic, entering the stomach by three ducts and extensively ramified in the mantle margin. No cnidocysts. Kidney not much branched. Hermaphrodite gland a single undivided mass: one spermatotheca: three genital orifices: no armature in the genitalia.

These characters do not agree with those given for any recognized family of nudibranchs. Superficially Doridoeides resembles Doridoxa (Bergh, 'Ingolf Expedition,' vol. ii, 1900, 'Gastropoda nudibranchiata,' pp. 15-19), but Bergh states that this latter has (1) a large blood gland, (2) a holohepatic liver opening into the stomach by a single opening, (3) a spermatocyst, although "its relation to the sperma-

totheca could not be determined." The affinity between the two genera is therefore not close. In structure Doridoeides is more nearly allied to Pleuroleura (= Dermatobranchus) but the general habitus and the configuration of the anterior parts and rhinophores is different, and unless intermediate links are discovered it is not clear that Doridoeides is either the ancestor or descendant of Pleuroleura. It must therefore be made the type of a new family Doridoeididæ, the characters of which are at present the same as those of the genus, but the absence of oral tentacles, the narrowness of the radula and the denticulation of the jaws are probably not of more than generic importance. The family belongs to the Cladohepatica. Its only anomalous characters are the doridiform shape (which is really not very different from that of the Pleurophyllidiidæ) and the presence of three genital openings. But, as Brüel observes ('Geschechts- und Verdauungs-organe von Caliphylla mediterranea,' Halle, 1904), although it is commonly stated that all the Æolididæ are simply diaulic, the data available do not justify so comprehensive a statement. It is nevertheless true that Doridoeides presents the arrangement of the genitalia which is typical of the Doridida, except that the second spermatotheca cannot be found. Although in that group the hermaphrodite gland usually takes the form of a layer spread over the liver, yet it is a separate mass (or masses) in Bathydoris, Alloiodoris, Doridoxa and Trevelyana.

Doridoeides is thus an annectant form connecting the Holohepatica and Cladohepatica, but having the essential characters of the latter, and its systematic position can hardly be fixed without reference to our general ideas respecting the phylogeny of the Nudibranchiata. The most definite view respecting this phylogeny is that put forward by Pelseneer ('Recherches sur divers Opisthobranches,' 1894). According to it the Tritoniidæ are allied to the Pleurobranchidæ, especially Pleurobranchæa. The Tritoniidæ are the common source of the Doridioidea and Æolidioidea, which

represent two lines of development in two different directions. The Elysioidea are derived from the Æolidioidea. Bergh has frequently expressed the opinion that our knowledge of the Opisthobranchiata is not sufficient for the formulation of any phylogeny, and his own views are so tentatively and undogmatically expressed that it is difficult to summarise them. In his 'System der Nudibranchiaten Gasteropoden' (1892) he appears to regard the Nudibranchiata as diphyletic, p. 996 ("Durch die Ascoglossen knüpft die eine Gruppe der Nudibranchien an die Aphysiaden und die Bulliden an, die andere durch die Pleurobranchiden wieder an diese letzteren"), the Æolids being nearest to the Ascoglossans, and the Tritoniidæ being derived from the Æolids by gradual reduction of the hepatic ramifications, as seen in Bornella, Dendronotus, and Scyllæa. In his article "Ueber clado- und holohepatische nudibranchiate Gastropoden" ('Zool. Jahrb. System.,' 1906, pp. 739—742), while still maintaining this view of the Tritoniidæ, he regards Tritonidoxa, Doridoxa, and Bathydoris as bridging over the interval between the Tritoniidæ and the Dorids or Holohepatica. It is not clear what is the relationship of the Holohepatica to the Pleurobranchidæ on this hypothesis, and it seems to be implied that the Æolids, which are a highly specialised type, lose their peculiarities and pass into the Tritonids, which are a comparatively generalised type, and that the Tritonids then develop a new highly specialised type, the Dorids. We find it hard to accept this view without stronger evidence than is forthcoming. The branching of the liver may disappear in some cases,[1] and the animal which forms the subject of this memoir might be regarded as a derivative of the Æolidiidæ which has retained its cladohepatic system and adopted a doridiform shape. But a consideration of the whole series of forms now known (many of which have been described only in the last ten years) inclines

[1] E. g. in Pseudovermis, and Trinchese states that in the larva of Lomanotus eisigi the æolidiform and cladohepatic characters are much more marked than in the adult.

us to believe that the holohepatic condition is the more primitive, and the cladohepatic condition derived from it, though it may make its appearance very early in the pedigree of the nudibranchiata. Further, if it is admitted that a comparatively unspecialised group (such as the Tritoniidæ) connects two highly specialised groups (such as the Æolidiidæ and the Doridídæ), the origin of the whole series is probably to be sought in or near the unspecialised group, and we therefore think with Pelseneer that Tritonia,[1] or rather some extinct allied form must be the ancestor of both the Holohepatica and Cladohepatica, and likewise nearly allied to the Tectibranchs.[2] Pleurobranchæa is certainly the Tectibranch which most nearly resembles the Holohepatica, but it does not follow that it is necessarily their direct ancestor, for the characters of the Pleurobranchidæ appear to be due to the shell being enclosed by the integuments, the asymmetrical ctenidium remaining; whereas in many nudibranchs, at any rate, the shell is rejected in the larval stage, not enclosed, no ctenidium is formed, but symmetrical respiratory organs of various types are developed instead. Nothing except the fact that the more primitive nudibranchs, as far as they are known, seem nearly allied to one another, renders it improbable that more than one type of larva may have adopted this method of development by rejection of the shell and symmetrical growth.

Are the more primitive nudibranchs those with or those without special gills? It will be well to review the principal gill-less forms more or less allied to Tritonia. It may be premised that all the Doridídæ appear to have pallial respiration (as also the Pleurobranchidæ) which is merely supple-

[1] Tritonia itself may have developed special features, such as its oral veil, tentacles, peculiar rhinophores, and branchiæ.

[2] This is without prejudice to the question of the derivation of the Elysioidea from the Ascoglossa. It seems to us possible that the Nudibranchiata (like the shell-less Pulmonata) may be polyphyletic, but that, if so, it is more likely that the Elysioidea have a different origin from the Æolids than that the Æolids have a different origin from the Dorids. But Myrrhine to some extent connects the Æolids and Elysioidea.

mented not replaced by the action of accessory gills. It may even be said that the Æolids and many other cerata-bearing Cladohepatica have nothing but pallial respiration, for the cerata and the hepatic ramifications which they contain are not so much special respiratory organs as a special disposition of other organs arranged so as to facilitate pallial respiration. But the following genera have neither this arrangement nor accessory gills.[1]

Tritonidoxa, Bergh.[2] Similar to Tritonia in all respects except that it has a broad, undulating dorsal margin without any trace of branchial tufts. Dorsal surface smooth. Size (32 mm.) moderate.

Tritoniella, Eliot.[3] Similar to the last genus, and like it resembling Tritonia in most peculiarities, but the dorsal margin, which is wide, bears simple unbranched prominences and not foliaceous tufts. The back bears ridges. Rather large (63 mm.).

Doridoxa, Bergh.[4] Doridiform in appearance and holohepatic. Blood gland and two spermatothecas. But there are no branchiæ, the anus is lateral, jaws are present, the

[1] We have not taken into consideration Pseudovermis or the Hedylidæ. The former appears to be a retrograde Æolid. The systematic position and relationship of the Hedylidæ are not clear. The same may be said of Timorella (Bergh, 'Siboga Exp., Opisth.,' p. 241, 1905).

[2] "Ueber clado- und holohepatische nudibranchiate Gastropoden," 'Zool. Jahrb. Syst.,' 23 Band, 6 Heft, 1906; and "Marine Investigations in S. Africa," vol. v, part i—Opisthobranchiata, pp. 86—88, in 'Trans. S. Afr. Phil. Soc.,' vol. xvii, 1907.

[3] Eliot, 'National Antartic Expedition (Discovery) Nudibranchiata,' 1907, pp. 5—11. Tritoniella seems generically distinct from Tritonidoxa since it has dorsal ridges and prominences on the dorsal margin. If the two genera are regarded as synonymous the name Tritoniella has priority. The description was published on March 5th, 1907, and the chief characters had already been named June 9th, 1905 (Eliot, 'Trans. R. Soc. Edinburgh,' vol. xli, part iii, No. 22, p. 525). The description of Tritonidoxa appeared on March 14th, 1907, the chief characters having already been named by Bergh in 'Zool. Jahrb. Syst.,' 23 Band, 6 Heft, 1906.

[4] In 'Danish Ingolf Expedition,' vols. 2, 3, 1900, "Nudibranchiate Gastropoda."

radula is about 36+1+36 and the hermaphrodite gland is separate from the liver mass. Small (12 mm.).

Heterodoris, Verrill.[1] Imperfectly described. Form like Triopa; no gills; back bearing papillæ and a longitudinal crest; rhinophores retractile; anus lateral (?). Radula 168. 0. 168. Jaws? Genitalia? Moderate size (28 mm.). This little-known form is possibly related to the Polyceradæ.

Charcotia, Vayssière.[2] Resembles the Tritoniidæ in form. Back tuberculate. Rhinophores not perfoliate and not retractile. A membranous expansion round the mouth. Jaws present. Radula 1+1+1. Liver divided into three glandular masses, but not passing (it would seem) outside the main body-cavity. Hermaphrodite gland mingling with the posterior liver mass. Small (14 mm.).

Phyllirhoidæ. A family of pelagic nudibranchs with no appendages except rhinophores. Jaws present. Radula varies from 1+1+1 to 11+1+11. Three or four hepatic coeca, not ramified. Hermaphrodite gland in several separate lobes.

Dirona,[3] MacFarland. Æolidiform in appearance, but the papillæ do not contain hepatic diverticula, and there are no branchial tufts. Liver trilobed but solid, wholly contained in body-cavity and not ramified. Hermaphrodite gland consisting of several separate lobes. Anus far back on right side. Jaws: radula 2+1+2. Small (19 mm.).

Pleuroleura, Bergh[4] (=Dermatobranchus, v. Hasselt). Allied to Pleurophyllidia, from which it differs only in having no branchial lamellæ beneath the mantle. Shape quasi-doridiform, but rhinophores and head parts modified, perhaps in connection with burrowing habits. Jaws: radula varying from 4+1+4 to 41+1+41. Liver ramified, and

[1] 'Trans. of the Connecticut Acad.,' vol. 2, 1882, pp. 548-9.

[2] In 'Expédition antarctique française du Dr. J. Charcot,' "Mollusques nudibranches et Marséniadés," 1906, pp. 27—31.

[3] See Cockerell and Eliot, "Notes on a Collection of Californian Nudibranches," 'Journal of Malacology,' 1905, pp. 45—48.

[4] See especially Bergh, "Die Pleuroleuriden," in 'Zool. Jahrb. System,' 3 Band, 3 Heft, 1888, p. 348 ff.

penetrating to mantle margin; cnidocysts present. One spermatotheca: hermaphrodite gland a single mass, separate from the liver. Most of the species are small. Some attain a length of 35 mm.[1]

Gill-less molluscs are on the whole smaller than the corresponding forms with gills, and the genera less numerous in species and probably in individuals;[2] but except for this the presence or absence of gills seems to make no difference, similar forms being found with and without them. A remarkable instance of this is seen in the Docoglossa. Acmæa has a ctenidium only; Scurria a ctenidium and a circle of accessory pallial branchiæ; Patellidæ the circle of pallial branchiæ only; Lepetidæ and Bathysciadium no branchiæ whatever. Yet all these forms seem to lead the same kind of existence, and to thrive equally well. Similarly in the Pteropoda we find Dexiobranchæa with only a lateral gill, corresponding to a ctenidium; Pneumoderma with this lateral gill and secondary terminal gills as well; Notobranchæa with these secondary branchiæ only; and Clione with no branchiæ at all.

In the other Opisthobranchiata the combination of a ctenidium with accessory branchiæ has not been recorded, but we find, though not within the limits of one family, Pleurobranchæa with a fully developed ctenidium, Tritonia with no ctenidium but with secondary pallial branchiæ, and Tritonidoxa with no branchiæ at all. The ctenidium in the Pleurobranchidæ does not show any sign of becoming vestigial[3] preliminary to its disappearance, and the suddenness of the change from the Tectibranchs to the

[1] On the hypothesis that the Elysioidea are derived from the Lophocercidæ, it is noticeable that gill-less forms make their appearance near what may be supposed to be the point of origin. In the Limapontiidæ the liver is not much ramified, and there is no trace of gills. In Elysia a number of ridges radiate from the pericardium, but hardly form branchial lamellæ; the liver is ramified in the wide lateral wings, much as in Doridoeides.

[2] But the Pteropod Clione is found in large shoals.

[3] In the Peltidæ (which appear not to be derived from the Pleurobranchidæ) the gill is small and simple.

Nudibranchs is perhaps explicable by the fact that the larvæ of the latter reject the shell before the gill is formed.

Now the absence of gills is certainly not a primitive condition in mollusca, and in many groups the gill-less forms are obviously specialized or degenerate. But the Nudibranchiata are admittedly derived from the Tectibranchiata by suppression of the ctenidium and, as parallel forms are found with and without secondary gills among the less specialized nudibranchs (e.g., Tritonia and Tritonidoxa), it may be that the gill-less forms remain as a record of the first weak effort to develop a new type which greatly increased in strength and variety by the acquisition of secondary branchiæ. Tritonia and Doris are clearly much more successful types than Tritonidoxa and Doridoxa and their superior respiratory apparatus may be the cause. On the other hand if the forms with gills are supposed to be the earlier, it is not obvious why so many families have lost their gills. The special conditions of pelagic and fossorial life might explain their disappearance in Phyllirrhoe and Pleuroleura (though Pleurophyllidia which has branchial lamellæ and is much richer in species than Pleuroleura, is also fossorial), but there is no obvious specialization about the other forms. Tethys (with pallial branchiæ) and Melibe (without them) are very similar forms, and in some respects Melibe seems the more archaic of the pair, since it possesses jaws which Tethys has lost. The question can be settled definitely only by the discovery of forms more primitive than those now known (that is to say, clearly intermediate between the Tritoniidæ and the Tectibranchs), and we merely wish to indicate the shape it assumes in the light of the interesting new genera recently discovered. Tritonidoxa and Tritoniella are little more than Tritonias without branchiæ: Doridoxa is a real connecting link, a Tritonid with many of the special characters of the Doridida. Dirona is a Tritonid with papillæ on the back, but the liver though lobed is not ramified: Charcotia also seems to

connect the Tritonidæ with some of the Æolidioidea but its affinities are less certain.

Doridoeides should probably not be regarded as a very primitive form. Its genital ducts are triaulic and the liver is elaborately ramified. Still, it obviously marks a stage when the characters of the Æolidiidæ, Tritonidæ and Doridæ could be combined in one form. The doridiform shape is probably not important morphologically: it occurs in very diverse families of Gastropods (besides nudibranchs, it is found in the Pleurobranchidæ, Oncidiidæ, Lamellariidæ and many Chitons) where the shell is absent or small, and it is probably largely due to mechanical reasons. The structure of the rhinophores is more significant. The jaws and radula are interesting for they show that these organs are practically the same in Bathydoris, Doridoxa, Tritonids, Doridoeides and Pleuroleura, the chief difference consisting in the width of the radula. Narrow radulas are characteristic of the more specialized Cladohepatica, except Antiopella (Janus), but also occur in some species of Tritonia (Candiella) and Pleuroleura. As Doridoeides is small, and no other form of the same structure is known, it may be presumed that Nature's experiment in making this combination of characters has not proved a success. The large number of æolidiform nudibranchs seems to show that the cladohepatic arrangement without accessory branchiæ answers better in active animals with dorsal appendages than in flat sedentary animals. The mantle margin of Doridoeides with the hepatic ramifications within it corresponds to the cerata of an Æolid, but is less extensive in surface, less mobile and therefore less efficacious for aerating.

As mentioned above, Doridoeides approaches most nearly to Pleuroleura of known nudibranchs, but the resemblances though important are somewhat general, and may be due to convergence. If a phylogenetic connection is accepted, the fact that both Pleuroleura, which is probably fossorial, and Doridoeides, which probably lives on

the leaves of seaweeds, are devoid of gills makes it likely that these gill-less forms are more ancient than Pleurophyllidia, and not retrograde.

Though Doridoeides is superficially not unlike Corambe (Doridella, Hypobranchiæa) it is not nearly allied to either the Corambidæ or the Phyllidiidæ. Both these families are holohepatic, and have a totally different arrangement of the mouth parts: branchial lamellæ situated beneath the mantle edge are found in all the genera comprised in them.

The heart and circulatory system of Doridoeides offer some points of interest. The heart lies somewhat to the right of a median line drawn longitudinally through the viscera, and the auricle adheres to the right wall of the pericardium. This may be a reminiscence of an earlier arrangement in which there was a ctenidium on the right hand side communicating with the auricle. The walls of the heart are thin, and in many sections the organ has an unsubstantial and shadowy appearance. The arteries also are thin, and hardly extend beyond the middle fifth of the body either backwards or forwards. They are developed most fully in the smaller specimens, and seem to atrophy as the animal grows. A similarly feeble development of the heart and circulatory system seems to occur in other gill-less nudibranchs. The Scaphopoda have neither gills nor heart. Kovalevsky[1] had some difficulty in seeing the heart in Pseudovermis and Hedyle, and could find it only in one species of the latter. In Tritoniella the heart lies to the right of the median line, and Bergh says of Pleuroleura ornata, "die aorta konnte nicht verforgt werden."[2] It would seem that in a gill-less mollusc the heart has no power of collecting purified blood and distributing it over the body, for the purification takes place all over the surface, not in a special organ. A strong pulsating machine and an extended

[1] 'Mémoires de l'Acad. Imp. des Sciences de St. Pétersburg,' vol. xii, Nos. 4 and 6.

[2] "Mal. Unters.," in Semper's 'Reisen.,' Heft vi, p. 284.

arterial system are, therefore, unnecessary. All that is required is sufficient movement to keep the blood from stagnating. But the extensive venous system is provided with valves which we have not noticed in other molluscs or seen described. They, presumably, serve to regulate and control the circulation.

EXPLANATION OF PLATES 15 AND 16,

Illustrating the paper by Sir Charles Eliot and Mr. T. J. Evans on "Doridoeides gardineri: a Doridiform Cladohepatic Nudibranch."

PLATE 15.

FIG. 1.—Doridoeides gardineri. *A.* dorsal, *B.* ventral view of whole animal. *a.* Mouth. *b.* Genital orifices. *c.* Anus. *d.* Accidental folds of foot. The specimen has been selected as showing the orifices, but in its natural shape the foot appears to be triangular, with a straight broad margin below the mouth.

FIG. 2.—Transverse section of dorsal body-wall.

FIG. 3.—Central nervous system of Doridoeides gardineri. *a.* Cerebro-pleural ganglia. *b.* Pedal ganglia. *c.* Eyes and olfactory ganglia. *d.* Buccal ganglia.

FIG. 4.—*a.* Jaw. *b.* Denticulate edge of ditto.

FIG. 5.—*a.* The radula seen from above. *b.* Side view of median tooth. *c.* Side view of first lateral. *d.* Side view of fourth lateral.

FIG. 6.—Alimentary system. *a.* Œsophagus. *b.* Anterior portion of stomach. *c.* Posterior do. *d.* Intestine. *e.* Right liver duct and branches. *f.* Posterior do. *g.* Left do.

PLATE 16.

FIG. 7.—*a.* Ventricle. *b.* Auricular ventricular valve. *c.* Auricle. *d.* Auricular extension. *e.* Aorta. *f.* Renal pericardial opening. *g.* Line of adhesion of auricle to ventricle.

FIG. 8.—Vein showing valvular construction.

FIG. 9.—Reproductive system. *a.* Hermaphroditic gland. *b.* Duct of do. *c.* Ampulla of do. *d.* Vas deferens. *e.* Penis. *f.* Bifurcation between male

and female branches. *g*. Spermatotheca. *h*. Vagina. *i*. Opening of mucus gland. *l*. Albumen gland. *m*. Mucus gland.

Fig. 10.—Section of hermaphrodite gland and adjoining parts. *a*. Male loculus containing spermatozoa in various stages of development. *b*. Female loculi. *c*. Do. showing communication with central male loculus. *d*. Dorso-ventral muscle bands passing through the hermaphrodite gland. *e*. Branches of the kidney. *f*. Section of main posterior liver duct.

Fig. 11.—Longitudinal section of whole animal, slightly to left of median line. *a*. Mouth. *b*. Radula sac. *c*. Anterior part of stomach. *d*. Posterior do. *e*. Spermatotheca. *f*. Ampulla of hermaphroditic gland. *g*. Duct of hermaphroditic gland. *h*. Hermaphroditic gland. *i*. Hepatic diverticula. *k*. Kidney. *l*. Blood spaces. *m*. Mucus gland. *n*. Salivary gland.

Fig. 12.—Transverse section of whole animal. Lettering as in fig. 11.